

Plasticity in Nesting Behavior of a Renting Wasp, and Its Evolutionary Implications. Studies on Eumenine Wasps, VIII (Hymenoptera, Aculeata)

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ABSTRACT

Ancistrocerus tuberculocephalus sutterianus (Saussure), previously known as a "renting" wasp (namely, a wasp that nests within preexisting cavities), is shown to be a facultative rather than an obligate renter. The wasp mined and masoned nests within a block of pith-like plastic, and it did so inside of a dark enclosure (≤ 0.8 lux = maximum illumination). Thus it can (and does) excavate nests of a strikingly different sort than those it commonly rents. Significantly, the excavated nests are quite similar to the supposedly primitive nests of certain ground-nesting *Euodynerus*.

Occupancy of a darkened enclosure is related to *A. t. sutterianus*' association with *Sceliphron*. Evolutionary aspects are discussed, and it is shown that current, favored methods for studying twig-dwelling wasps must tend to bias results. Contrary to common belief, facultative renters are very likely a numerous class among eumenids, obligate renters comprising a small or empty one.

The striking behavior and nests of *Ancistrocerus tuberculocephalus sutterianus* (Sauss.) to be described have no parallel in what has been recorded for this species or, as far as I am aware, for any other of the many nearctic eumenid wasps known to occupy trap nests. Both *A. tuberculocephalus tuberculocephalus* (Sauss.) and *A. t. sutterianus* are "renting" wasps; that is, they are known to construct nests in small preformed cavities and in open burrows in wood, whether natural or artificial (Rau 1940, Bequaert 1944, Bohart [in Muesebeck *et al.* 1951], Barr [in Ferguson 1962], Parker 1962, Parker and Bohart 1968, Krombein 1967, Goodpasture 1974). Is "renting" obligatory for *A. tuberculocephalus*—is that the limit of its nesting behavior and capability?

As neither subspecies is known to mine in the ground, to burrow in plant stems, or to construct free nests of mud, each a regular but different mode of nest construction employed by particular eumenines, it may seem idle to wonder what sorts of nest *A. t. sutterianus* would or could construct were it not to "rent."

The eleven nests to be described give ten direct, surprising answers to that question.

The behavior that led to construction of the nests of *A. t. sutterianus* (Riverside, California) is unusual in two main respects: (1) the nests were made within a dark, nearly completely enclosed space of approximately 0.02 m^3 (0.68 ft^3), namely within a box with tight walls, and (2) they were made in a solid block of plastic having a pith-like consistency.

The box, mounted on a masonry wall 112 cm (3'8") above the ground, was open only on the underside by an irregular hole roughly 5×2 cm (1.6 in^2). Illumination within the box was by reflection through the hole from the earth below, reduced by an internal baffle to a level at the nesting site at midday of only 0.5–0.6 lux, reaching a peak of 0.8 lux in the early afternoon. Subjectively 0.5–0.6 lux corresponds with summer dusk about one-half hour after sunset and is near the absolute threshold (0.26 lux) of the completely dark-adapted honey bee (Autrum and Seibt 1965). The exposed soil below the box, regularly dampened by a slight seepage each evening, apparently served

as source of mortar used by the nesting wasp.

The Nesting Substrate

The nests were constructed in a 20 cm × 18 cm × 25 mm-thick block of white styrofoam[®] placed furthest from the entrance, against the left inner wall of the box. The block served to hold unused control pins (of a timing device), the pins being inserted in a horizontal row near its upper edge. One pin, however, had fallen from the plastic, leaving an irregular hole. On August 18, that hole was found to have been covered with a dab of mud; elsewhere on the formerly unbroken vertical surface of the styrofoam, well below the line of inserted pins, there were ten other scattered pats of mud.

The Nests

The dabs of mud marked the closure of a nest of *Ancistrocerus t. sutterianus* in each case. Burrows of ten of the eleven nests had necessarily been initiated and excavated by a female wasp, for they were constructed where no pins had pierced a passage into the styrofoam. The control pin that had fallen from its hole must have left a broken surface and an only partially open, horizontal passage about 17–20 mm long × 0–2 mm wide, irregularly compressed into the styrofoam (to judge from those perforations left by the other pins when removed). That narrow, ill-shaped hole had been greatly widened and modified by the founding wasp to form a single-celled nest (fig. A). The construction of that nest differed in no obvious way from those of the five other one-celled nests (figs. B–F), even though it alone had been excavated along the line of a preformed passage. The wasp that emerged from that nest had done so before the nests were discovered in mid-August, 1976. To judge from the dimensions of its provisioned cell (table 1, A), the occupant almost certainly had been a male.

The eleven nests had in common (1) a covering cap, somewhat ellipsoidal or circular in shape, rough on its surface and

generally but not always (e.g. figs. B, D) somewhat convex, (2) an entrant passage, largely filled with the mud of the cap but in no case partitioned by a special wall to form a vestibular cell, and (3) one or two cells, dug with the major axes very roughly normal to the entrant passage. In only two cases (cells I-1 and K-1) was the bottom of a cell not veneered with mud to form a smooth, concave floor; in neither of these had that cell been provisioned by the wasp, nor had an egg been attached to its wall. Each of the five two-celled nests (G–K) had a complete mud partition separating the two provisioned cells. The outer surface of the partition that faced the upper cell was smooth and concave, the inner surface (forming the roof of the bottom cell) was rough and convex, as usual in eumenine nests and so important for the survival of individuals and species (Cooper 1956, 1957; Tsuneki and Moriyama 1973).

The cocooning larvae, having thrust the remains of the caterpillar prey and their fecal pellets below, had coated the surfaces of their cells with “varnish” and silk. The cocoon of the parasitic wasp *Chrysis (Tetrachrysis) coerulans* Fabr. in nest D was free, nevertheless the walls of that cell also had been lightly “varnished” and very loosely webbed.

Measurements, ratios, and estimates (as areas and volumes) of components of the nests are given in Table 1. There is little quantitative fidelity in either one-celled or two-celled nests, a fact well reflected in the very large coefficients of variation of the linear measurements that range from 13 to 79 for rank-1 nests, 15 to 66 for rank-2 nests. Nor do features of individual nests, such as attributes of the cap, length of passage, size of cell, depth of nest or cell correlate in any obvious way with dates of emergences from the nests. The only clear relation is that the necessarily younger wasp of each fully-provisioned two-celled nest had emerged before its elder, the older wasp in each case having developed in the larger bottom cell.

Such structural regularities as do occur are all familiar architectural features

Table 1.—Nests of *Ancistrocerus tuberculocephalus sutterianus* (Sauss.) excavated in a styrofoam block, ranked in order of cell number and date of emergence and lettered to correspond with figures. One-celled nests = A through F, 2-celled = G through K (lower cell = 1, upper = 2). Linear measurements and thickness (θ) in mm, areas in mm², volumes in mm³ (all decimals rounded). Cap asymmetry = length: width; masonry at base of cell = maximum thickness of mud liner of single and bottom cells, and cross wall of 2-celled nests. Nest depth is the greatest vertical distance excavated from the surface of the styrofoam. CV = coefficient of variation for linear dimensions.

Fig.	Emerg'd		Cap			Passage		Nest depth	Cell		Masonry		Exit hole Dia.	Ratio V wasp: V cell
	Sex	Date	Area	Asym	θ	L	W		Vol	L:W	base cell-1	cross wall		
A	?	8/18	79	1.4	6.2	5.2	4.3	11.4	181	1.1	0.8	—	3.6	?
B	♂	11/20	37	1.2	1.0	1.0	4.8	9.0	123	1.9	1.5	—	2.8	0.2
D	?	3/18	30	1.0	3.0	4.6	4.5	11.5	231	1.4	1.5	—	?	—
F	♂	3/19	35	2.0	2.8	2.0	3.5	9.5	105	1.6	0.1	—	?	0.3
E	♂	3/23	23	1.5	5.5	5.0	3.5	11.0	170	1.5	1.0	—	?	0.3
C	♂	3/23	87	1.4	3.0+	6.0	4.0	14.0	170	1.5	0.1	—	?	0.5
CV					53.4	50.1	13.0	16.0			78.8			
H			37	1.0	1.3	1.0	5.0	12.5					4.4	
2	♂	11/13							179	1.4		1.0		0.3
1	♂	11/16							188	1.7	1.8			0.4
G			34	1.2	2.7	3.0	3.5	18.5					3.6	
2	♂	11/13							204	1.4		1.0		0.2
1	♂	11/18							230	2.3	0.8			0.4
J			49	1.1	3.7	3.0	4.5	16.0					4.0	
2	♂	11/20							198	1.8		4.0		0.3
1	?								247	2.4	0.5			?
K			91	1.1	5.5	3.5	5.0	18.0					3.5	
2	♀	<12/30							466	1.2		1.6		0.2
1	O ²								118	1.8	0			—
I			37	1.2	3.5	1.5	4.0	11.5					—	
2	O ²	—							28	2.0		2.0		
1	O ²	—							59	1.8	0			
CV					46.4	45.2	14.8	19.2 ³			65.9 ³	64.5		

¹ The wasp had emerged before the suite of nests was discovered.

² Unprovisioned cells; those of I-2, I-1 are clearly too small for rearing, the nest is abnormal and its bottom cell contained the shriveled remains of a walled-in spider.

³ CV for nest depth estimated for cells of H, G and J only, known to be those of males—or probably so (cell J-1).

regularly found in linear nests of eumenids constructed in hollow twigs or in trap nests of which the outer walls limit cell shapes: (1) the first provisioned cell is larger than any subsequent provisioned cell; (2) the base of the first cell is smoothed with mud into a regular concavity if otherwise it would be irregular, and if that cell is a provisioned one (compare the unprovisioned basal cells of nests I and K with all other basal cells); and (3) cross walls are smooth and concave where facing the exit of the nest, rough and convex on the reverse side. Finally, the sole cell from which a female wasp

emerged is by far larger than any of the nine cells from which males emerged.

The Sex Ratio

The observed sex ratio is 9 males to 1 female. Two of the original brood died as larvae and were not sexed, so the probable primary sex ratio for this family cannot be less than 9 males to 4 females or more than 12 males to 1 female (for the sex is unknown of the wasp that emerged prior to discovery of the nests), namely from 69 to 92% males. Possibly these nests were made by a female with

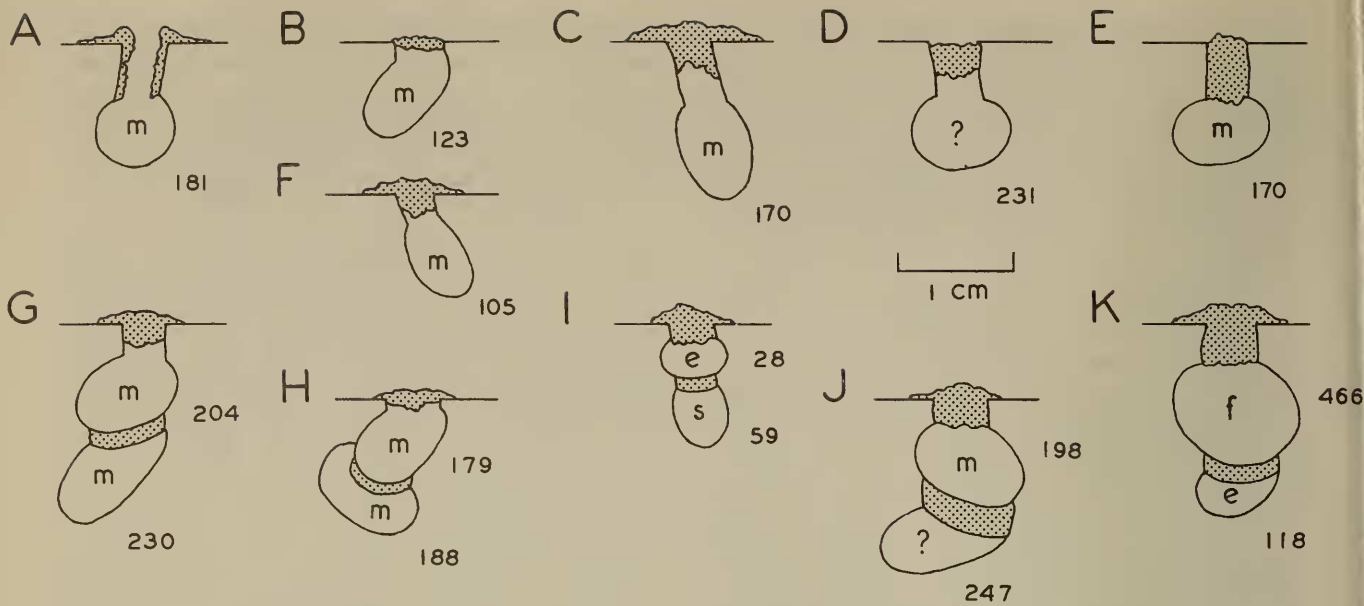


Fig. 1. A–K, diagrams of nests excavated by *Ancistrocerus tuberculocephalus sutterianus* (Saussure) in styrofoam. All nests were dug normal to the vertical surface of the plastic; mud closures and cross-walls hatched (see text and table for details); volume, in mm³, noted to lower right of each cell; sex of occupant of each cell indicated where known; *Chrysis coeruleans* Fabr. emerged from D; pharate pupa accidentally destroyed in J–I; e = empty cell, f = female, m = male, s = dead spider; scale = 1 cm.

a nearly exhausted supply of sperm, for available records from rearings of *A. t. sutterianus* suggest a less skewed ratio, thus 9 males, 0 females (Bequaert 1944), 37 males, 43 females (Parker 1962), 6 males, 3 females (Goodpasture 1974), and 3 males, 1 female (Cooper, unpublished), for a total of 55 males to 47 females, or 54% males. Nevertheless, it cannot be guessed whether that ratio is close to the primary one or not, for only Bequaert and I have recorded the total number of provisioned cells involved.

Krombein (1967) reports that 86 stored cells of *A. t. tuberculocephalus* gave 43 males, 5 females, with 38 cells failing to produce adults, of which *most* were judged by Krombein to have been those of males on the basis of cell dimensions and position in the linear nests. Krombein's observations gave lower (43 males, 43 females) and upper (81 males, 5 females) bounds for the sex ratio of 50% and 98% males, with 50% very probably far too low. In any case the range for the nominate species includes the estimates for my eleven nests of *A. t. sutterianus*. The strongly skewed sex ratio observed is thus not likely to be attributable to limitations placed on cell size or on

nidification by peculiarities of the nesting-substrate. It may, however, prove a function of the particular portion of the nesting period during which the nests were made; for example, Krombein's nests and those made in styrofoam probably represent samples from near (or at) the close of the nesting period.

Discussion

Excavation of the nests was not seen, so it cannot be proven that the eleven nests were all constructed by a single female (although believed to be so). Indeed it is known only that the nests were built not later than the close of July. Emergences were not clustered, but scattered over a period of at least seven months (Table 1). Such irregular emergence does not require the progeny to be that of more than one nesting female. Krombein (1967) records a nest of *Ancistrocerus t. tuberculocephalus* that took more than a year for the emergence of all occupants, and I have observed occasional nests of *A. antilope* (Panzer) with mixtures of diapausing and not diapausing individuals (see Nielsen 1932 for similar records). But either way,

whether nests of one female or more than one, the observations bear importantly on the adaptive plasticity of this eumenine wasp, and probably on that of many others.

It is striking that a founding female of *A. t. sutterianus* explored a darkened, spacious enclosure as a possible nesting site, an enclosure in which the maximum illumination attained was only 0.8 lux (at about 1300 hours Standard Time). That behavior is quite unlike what has commonly been recorded for other eumenids, but it assuredly must prove adaptive if finding old nests of *Sceliphron*, suitable for renovation, is now a significant feature of this eumenid's ecology as it seems to be (Bequaert 1944, Bohart [in Muesebeck *et al.* 1951], Goodpasture 1974, Parker [*in litt.*]). Species of *Sceliphron*, including *S. caementarium* (Drury) (Shafer 1949), frequently make their mud nests in shaded, or even dimly lit situations. For example, *Sceliphron* have been recorded by Fabre (1891) as having constructed nests within a narrow-mouthed gourd on the mantlepiece of a farmhouse, as well as within the depths of stone piles; Ferton (1908) took a nest from beneath a large stone; Dutt (1913) and Williams (1945) found nests in hollow trees, and indeed Iwata (1976) holds *Sceliphron deforme* Smith may at times ". . . prefer dark wall corners within closets" of houses. Thus search of a darkened space probably does not represent a behavioral quirk of the female (or females) that made the nests in styrofoam; it is viewed as one behavioral component involved in the common association of *A. t. sutterianus* with abandoned nests of *S. caementarium*.

A second striking fact is that *A. t. sutterianus* does not have a strongly stereotyped nesting routine. Maindron (1882) classified eumenids into three categories of nesting types: (1) constructors of masonry enclosed cells, (2) burrowers (mainly into soil), and (3) occupiers and renovators of preexistent burrows or cavities, namely "renters" as Iwata (1942, 1976) and others call them. Renting ordinarily minimizes the effort of

nest construction, thus providing a reduction in the wasp's energy budget (as Roubaud 1916 and Malyshev 1917 pointed out) even though the preexistent burrow may require modification to its needs as in Rau's (1928) record of *Ancistrocerus antilope* (Panzer) enlarging a burrow of *Ceratina* in sumach pith. When modification requires cutting out pith, as in that case, the renting wasp demonstrates a capacity that should permit it to construct in entirety its own nest in suitable, unworked pithy stems. Were renting long established, with available preformed burrows regularly exceeding demand and now the exclusive abode of a species, selection would be expected to favour maintenance of those abilities required for renovating hollowed stem nests or modifying available mud nests (since widening or reworking may often be required). There would be no such pressure, however, to maintain any genetic basis for instinctive construction of an entire nest in the absence of an available preformed burrow or cavity. An expected evolutionary result would be species of wasp that have become obligate renters.

Before the large number of observations now on record had been obtained, it was quite generally believed that the eumenids include many species which regularly mine soft wood and pith, constructing nests in their entirety, in contrast to others, also nesting in burrows, that habitually rent. There are, however, few cases (if any) on record where this may now be taken to be so, for all established burrowers in pith and wood known to me appear in fact to be facultative renters that readily accept suitable, preformed cavities as nesting sites. Among eumenines they include at least the African *Rygchium marginellus* (Fabr.) (Roubaud 1916), the Formosan *Nortonia kankauensis* Schult. (Iwata 1939, see Iwata 1976), and the European *Gymnomerus laevipes* (Schuckard) (Blüthgen 1961, Danks 1971b), *Pseudomicrodynerus parvulus* (Herrich-Schaeffer) (Blüthgen 1961), *Microdynerus helvetius* Sauss. (Enslin, 1922), *M. exilis* (Herrich-Schaeffer) (Blüthgen 1961; Danks 1961b) and *Ancistrocerus parietinus*

(Linn.) (Maindron 1882; Blüthgen 1961). Among raphiglossines certain species of *Rhaphiglossa* (see p. 250, Iwata 1976) and *Psiloglossa algeriensis* Saunders (Ferton 1920) have also been shown to be facultative renters. Indeed facultative renters may be a much larger class among eumenids than now suspected, including fabricators of masonry-enclosed cells as well as species that burrow in soil, in plant stems, etc. Except perhaps for very common species, however, facultative renting will not often be recognized as such for two principal reasons: (1) the very useful hollow trap-nest technique, as now so widely employed, permits only a test of the faculty for renting and, in some cases, for modifying existing burrows; (2) when a naturally occurring nest is found within an earlier abandoned masonry nest, or in a burrow within which there are unmistakable signs of prior occupancy, it is quite correctly concluded that a prefabrication has been used, namely that the nest is in fact a "rented" one. However, in the latter case all or most other natural nests of that species thereafter automatically become suspect as a rented nest even in the absence of clear evidence of earlier occupancy. For example, Krombein (1959) obtained a series of seven natural twig nests of *Leptochilus republicanus* (Dalla Torre). One among them had clearly been rented, for a dead *Ectemnius* (a crabronid) was found at the bottom of that nest; the origins of all six others therefore come into doubt! Is *L. republicanus* a facultative renter, or an obligate one as Parker (1966) believes to be the case for all twig-dwelling *Leptochilus*? With luck, traps of blueberry stems, rose stems, sumach and elder twigs, etc., having an intact central pith and set out where wasps abound, as Danks (1971a) appears first to have done in a systematic way, might give an answer in this and other cases.

In any case the evidence presented proves *A. t. sutterianus* to be a facultative renter. Furthermore the nests it constructed in the soft plastic have a special significance. All eleven are less like nests

of a typical stem nesting eumenine than they are similar to nests of a primitively ground burrowing eumenine, *Euodynerus crypticus* (Say), described by Isely (1914), Rau and Rau (1918), Turner (1922) and Vest (1936) under the name *Odynerus dorsalis* Fabr. (see Bohart and Menke 1974). The encircling hard outer wall of a plant stem of course limits to a cylindrical hollow the shape that can be given to a cell by a wasp whose body's cross-section is but slightly less than the diameter of the pith cavity. The nests in styrofoam, however, had no lateral limitations placed upon their construction, although the depth to which they could be constructed could not exceed 25 mm unless the wasp curved its entrant burrow from the horizontal plane (as many aculeates that burrow into clay banks do, but which it did not do). Unlike the described nests of *E. crypticus*, that were dug more or less vertically into hard soil (first moistened and softened by the wasp), and which frequently had a vestibular space, those of *A. t. sutterianus* were tunnelled horizontally, and no vestibule was made. In all else, however, though made in substrates of markedly different textures, hardnesses and necessarily modes of working, the nests of the two species are closely similar in design. Thus entrances are normal to the surface, or nearly so; ovoid cells are wider than the entrant burrows, with long axes not in line with the entrant burrows, and in tandem when there is more than one per nest for there are no lateral offshoots; separations of cells are by mud partitions, with the bottom provisioned cell of multicelled nests the larger. What is more, the nesting *A. t. sutterianus* removed the excavated pellets of plastic from the interior of the box, just as *E. crypticus* scatters its earthen pellets remote from its burrow's entrance. All of which gives emphasis to Evan's (1977) observation that in Eumenidae certain aspects of nesting behavior, location and type of nest "are not closely correlated with generic divisions based on structure."

Thus *A. t. sutterianus* is not an obligate renter, even though heretofore it has been

known exclusively as an occupant of empty nests of other aculeates, preformed burrows and trap nests. It is fully capable of constructing a nest in entirety in the absence of a suitable cavity and, when it does so, it surprisingly may exhibit what is widely considered to be a primitive nesting behavior and nest pattern (e.g., Evans and Eberhard 1970, Iwata 1976). It seems likely that available free or abandoned cavities suitable for occupancy do not regularly exceed demand, that on average both intra- and extraspecific competition for them must occur and, therefore, that selection still favors retention of primary nesting capability and behavior. Very likely *A. t. sutterianus* is not unusual among renting eumenids as a facultative renter (consider the cases cited above). Indeed the class of *obligate* renters, now regarded as largest of all, may prove to be a small or empty one, literally an artifact of the common current use of hollow trap nests. As with *A. t. sutterianus*, nesting routines of many species are probably less rigid than now believed to be the case, at least among eumenids that rent. Seemingly "atavistic" patterns may be expressed adaptatively under circumstances departing from those provided by hollow trap-nests and other preformed cavities, hence from what is now believed to be customary. Interestingly, Tsuneki and Moriyama (1973) point out a similar persistence of atavistic attributes as explanation of the appropriate responses by *Discoelius japonicus* Perez (a leaf-cutting eumenid) to cues that are included in the mud walls of nests made by wasps of other, widely different species, for orientation of pupae toward a nest's exit.

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